

DISTRIBUTION AND ABUNDANCE OF *HALOBATES* SPECIES (INSECTA: HETEROPTERA) IN THE EASTERN TROPICAL PACIFIC

LANNA CHENG¹ AND ERIC SHULENBERGER²

ABSTRACT

Halobates specimens were sorted from 1,649 surface neuston samples collected from the eastern tropical Pacific Ocean. At least one specimen was captured in each of 498 samples. Only 34 samples contained more than one species of *Halobates*. Four species, *H. micans*, *H. sobrinus*, *H. sericeus*, and *H. splendens*, were found in the eastern tropical Pacific area. The abundance estimates (lower bounds) range from 400 to 10,000 per km². Detailed zoogeographical distributions of the four species are presented. *Halobates micans* is a warmwater cosmopolite found between lat. 20° N and 20° S; *H. sericeus* appears to be confined to the central watermasses of the North and South Pacific and does not occur in the zonal equatorial currents; *H. sobrinus*, the most abundant of the four, is confined to the equatorial upwelling regions off the west coast of Central America; and *H. splendens*, the rarest species, appears to be associated with the central South Pacific watermass or the South American west coast current system. Although there is considerable overlap in the absolute geographical ranges of the three more abundant species, the regions in which they are abundant are almost entirely separate. Whether this is due to biological or physical processes is unknown.

Five species of the genus *Halobates* Eschscholtz (Insecta, Heteroptera: Gerridae), popularly called marine "water striders" or "sea skaters," are the only known insects whose normal habitat is the high seas. These pelagic insect plankters occupy an unique, truly two-dimensional environment. They are not known to penetrate below or rise above the surface (no winged forms are known for any *Halobates* species; Cheng and Fernando 1969). *Halobates* spp. spend their entire life cycle at the air-sea interface, and may therefore provide us with an unique opportunity to use them as biological tools for investigating air-sea and surface phenomena.

The peculiar habitat of oceanic *Halobates* spp. precludes their capture (except accidentally) by standard zooplankton or water-sampling equipment, and presents interesting questions of zoogeography and in the evolution of species. The occasional oceanic *Halobates* specimens found in conventional plankton samples made with submerged nets have shown that the five oceanic species are widely distributed on a scale of ocean-basin magnitude (Herring 1961; Savilov 1967; Scheltema 1968; Cheng 1973a, 1974). Although the ranges of distribution of the Pacific *Halobates*

spp. have been broadly defined by Savilov (1967), there have been few data for these insects from the southeastern Pacific; furthermore, no detailed quantitative study has hitherto been made on the sea skaters in the Pacific Ocean. An unique series of surface samples collected during the EASTROPAC survey enabled us to carry out an extensive study of *Halobates* spp. in the eastern tropical Pacific Ocean. We present here a detailed description of mesoscale (several hundreds of kilometers) zoogeographic patterns of four *Halobates* spp. in the area, as well as information on abundance, cooccurrence of species, and temperature effects on occurrence of species.

Various aspects of the biology of *Halobates* spp. are described in the literature. The taxonomy of the genus is reasonably well understood (Herring 1961). All 42 species described are to some extent associated with saltwater—mostly brackish waters or nearshore marine habitats. Some are confined to island groups or nearshore lagoons, estuaries, or bays (Cheng 1973a; Andersen and Polhemus 1976). Only five *Halobates* species (*H. micans* Eschscholtz, *H. sericeus* Eschscholtz, *H. sobrinus* White, *H. splendens* Witlaczil, and *H. germanus* White) are truly high-seas animals. Special adaptations of pelagic *Halobates* to its peculiar habitat include: 1) an ability to lay eggs on flotsam (Cheng 1974); 2) a cuticle with a microhair layer which traps air and prevents the

¹Scripps Institution of Oceanography, University of California, La Jolla, CA 92093.

²San Diego Natural History Museum, P.O. Box 1390, San Diego, CA 92112.

insects from being wetted by rain, spray, waves, and accidental submergence (Cheng 1973b; Andersen 1977); 3) a highly UV-absorbent cuticle, presumably to prevent chromosomal damage (Cheng et al. 1978); and 4) an ability to store relatively large amounts of food as triglycerides which their brackish-water and freshwater relatives are not known to possess (Lee and Cheng 1974). To date, attempts to rear pelagic *Halobates* in the laboratory have failed. Our knowledge of these insects is thus based upon analyses of preserved samples and on short-term observations or experiments carried out at sea. The present data are from an extensive set of neuston samples taken during the EASTROPAC investigations, which allows us to examine some aspects of species distribution and cooccurrence in relatively fine spatial detail.

METHODS

Present samples were collected during the EASTROPAC project, which surveyed the eastern Pacific between lat. 20° N and 20° S from the west coast of the American continents to about long. 120° W. There were seven cruises between January 1967 and April 1968, each of about 2-mo duration. Figure 1 presents areas surveyed for most of these cruises; some cruise tracks were complex, and areas surveyed and cruise length differed from cruise to cruise: details of cruise tracks are available (Fishery-Oceanography Center,³ and figures 10-70 TC in Love 1972 [EASTROPAC Atlas, Vol. 1]). The results of some of the biological, chemical, physical, and meteorological measurements have been published in several EASTROPAC Atlases (Love 1970-75) and elsewhere (Ahlstrom 1971, 1972; Tsuchiya 1974).

The neuston nets used to collect our samples filter only the top few centimeters of water, but may occasionally skip out of the water ("porpoising"; see Cheng 1975a). Moreover, to some extent, *Halobates* is able to detect and avoid such a net both visually (Cheng 1973c; Cheng and Enright 1973) and by receiving tactile warnings of its approach (Wilcox 1972). Consequently, the samples yield at best only semiquantitative data on *Halobates* and other pleustonic organisms (Cheng 1975a).

All the samples were replicates; a 505 μm mesh net with a circular mouth 1 m in diameter was towed half submerged at about 3 kn (≈ 1.5 m/s) for 20 min. Optimally, such a tow sweeps a path 1 m wide and 1,800 m long. Abundance of *Halobates* spp. is treated as number of individuals caught per standard tow; such a tow covers an area of about 1,800 m². However, our use of 1,800 m² as the "area per tow" is conservative, because both porpoising and variable depth of submergence will decrease the actual area covered. Possible avoidance by *Halobates* makes our abundance estimates even more conservative. Samples were preserved in 70% ethanol. Of 1,649 surface samples, 498 contained at least one *Halobates* individual. A total of 3,236 individuals were identified to species (Cheng 1975b). For each sample, we recorded the number of adults and nymphs; nymphs were identified to developmental stage and final instar nymphs and adults were sexed. Detailed information on the cruise series, the total number of surface tows made during each cruise, and the number of positive tows (i.e., containing *Halobates*) are presented in Table 1.

TABLE 1.—EASTROPAC cruise series, number of surface tows made, and number of tows containing *Halobates* spp. (1967-68).

Series number	Cruise Inclusive dates	No. surface tows	
		Total	With <i>Halobates</i> spp.
11	24 Jan.- 6 Mar.	120	67
12	7 Feb.-24 Mar.	118	41
13	20 Jan.-31 Mar.	141	42
14	21 Jan.-10 Apr.	98	25
20	10 Apr.-31 May.	128	52
30	14 June- 2 Aug.	127	26
47	31 July-29 Sept.	156	24
45	3 Aug.-25 Sept.	85	32
50	16 Oct.- 3 Dec.	120	36
OP ¹	13 Nov.- 2 Dec.	49	9
60	18 Dec.- 5 Feb.	124	31
76	19 Feb.- 5 Apr.	101	40
77	20 Jan.-28 Apr.	157	39
75	15 Feb.-15 Apr.	125	34

¹First digit of cruise number denotes the series, except for *Oceanographer* which is a "ship of opportunity" used in series 50.

RESULTS AND DISCUSSION

Species Distributions

Worldwide distributions of oceanic *Halobates* spp. have been presented by Herring (1961), Savilov (1967), and Cheng (1973a, 1974). Updated worldwide distributions of the four oceanic species which occur in the EASTROPAC area are shown in Figure 2. The general distribution of *Halobates* spp. resembles known large-scale plankton dis-

³Fishery-Oceanography Center, 1966-69. EASTROPAC Information Paper no. 1-11 (available from National Marine Fisheries Center, P.O. Box 271, La Jolla, CA 92038).

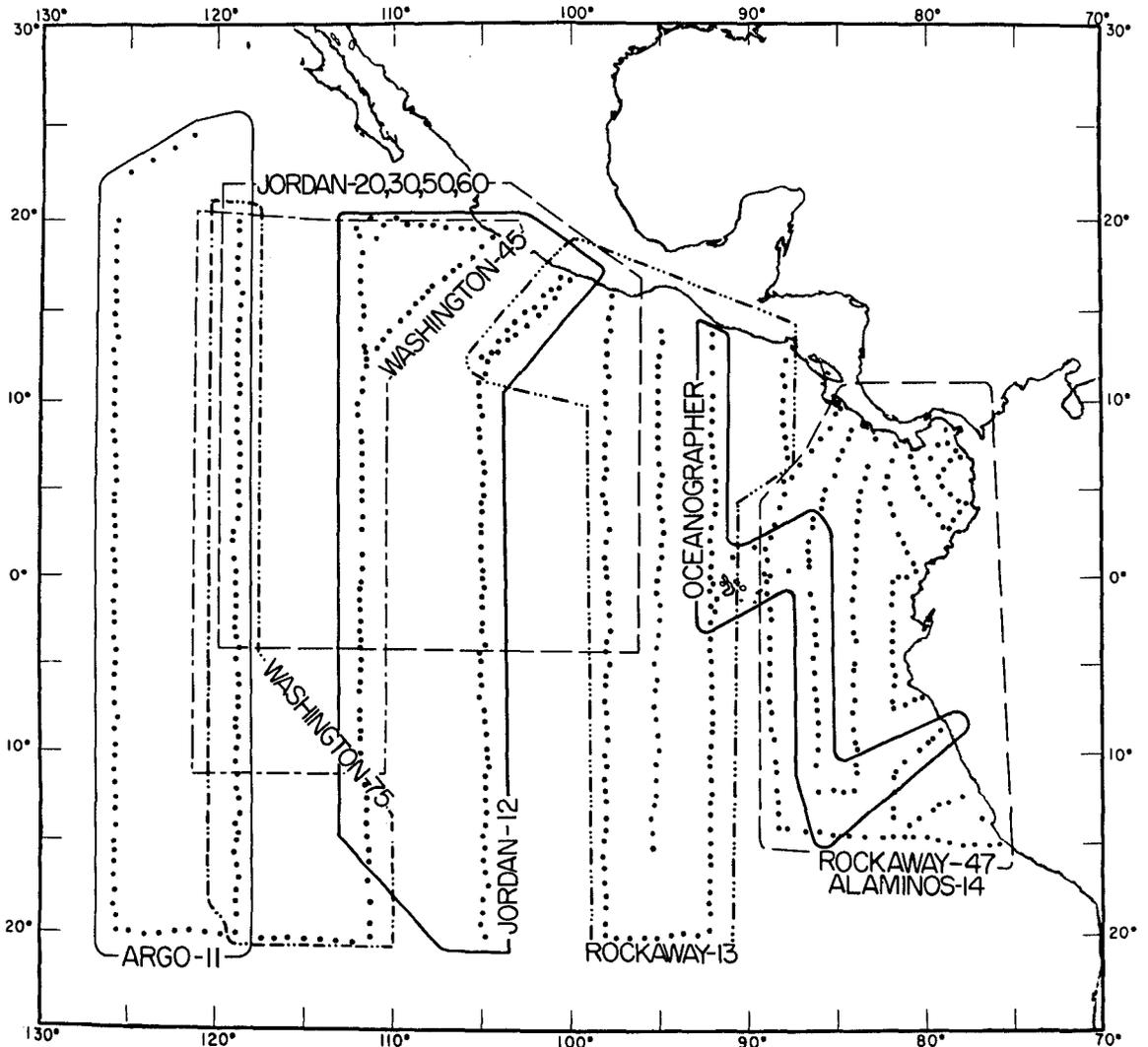


FIGURE 1.—General cruise tracks for the EASTROPAC Investigation showing basic station positions and areas covered during each cruise. Detailed data given in Table 1; exact station positions differ slightly from cruise to cruise.

tribution patterns, e.g., the eastern tropical Pacific, transition zone, central watermass, warmwater cosmopolite, and equatorial distributional patterns found by McGowan (1971, 1974), Reid et al. (1978), and Brinton (1979). These patterns seem to parallel the general surface circulation of central gyres, equatorial zonal flows, and eastern-boundary upwelling areas at the Equator (Sverdrup et al. 1942). No *Halobates* spp. is known to occur regularly at high latitudes.

Halobates micans is clearly a cosmopolitan tropical species occurring in all the world's equatorial current regions (Figure 2). Specimens occur at

latitudes higher than about 40° (lat. 55° S, long. 45° W and lat. 52° N, long. 36° W in Figure 2a) only where poleward extensions of strong warm surface currents are known (e.g., Gulf Stream and Kuroshio).

The North and South Pacific central gyres and the South Atlantic central gyre do not appear to contain *H. micans* in contrast to the North Atlantic central gyre (Figure 2). The central North Atlantic is more heavily sampled than any of the other three gyres; however, there are hydrographic reasons to believe that the results are valid, independent of sampling density. The Gulf Stream

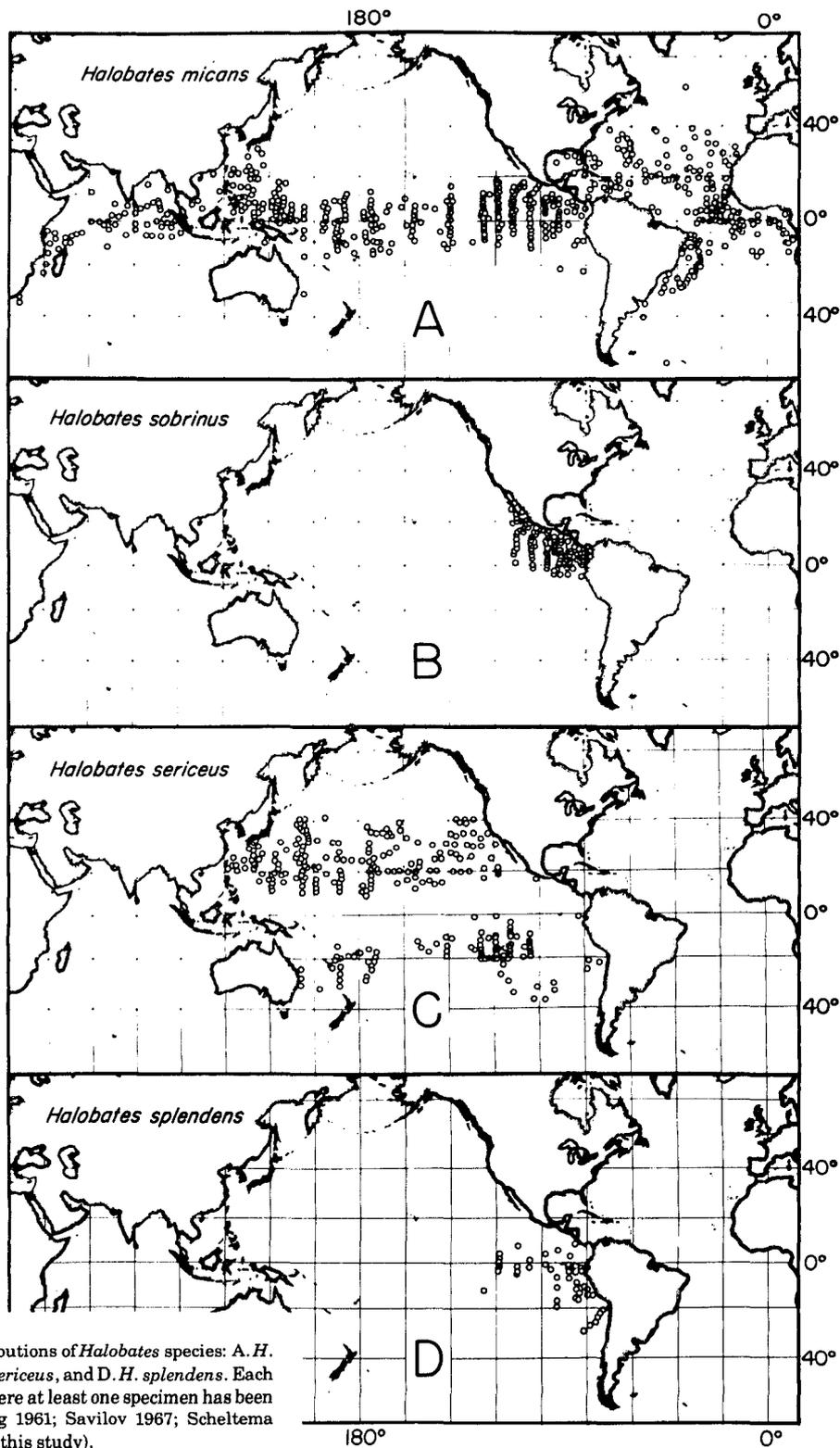


FIGURE 2.—Worldwide distributions of *Halobates* species: A. *H. micans*, B. *H. sobrinus*, C. *H. sericeus*, and D. *H. splendens*. Each circle represents a position where at least one specimen has been collected. (Data from Herring 1961; Savilov 1967; Scheltema 1968; Cheng 1974; and Cheng this study).

much like that seen in the western North Atlantic. This is because the general circulation patterns of the North Atlantic and the North Pacific are similar, and the scattered records in the western mid-latitudes in the North Atlantic are probably a result of the Gulf Stream.

In the eastern tropical Pacific, *H. micans* does not often occur south of lat. 10° S or north of lat. 20° N (Figure 3). The southern border of its distribution is well defined by the EASTROPAC sampling program. The northern border could be an artifact of that sampling program, since distributions of both samples and the species approximately coin-

cide. However, many negative EASTROPAC samples were taken north of the edge of the species distribution (Figure 3), a large number of California Current samples have also been negative for the species (Cheng unpubl. data), and other sampling programs have shown the same feature (Figure 2). These combine to convince us that the northern border shown in Figure 3 is not artificial.

Halobates sobrinus seems to be confined to the equatorial upwelling regions off the west coast of Central America, with some northward extension along the Mexican coast (Figure 2). Although both the North and South Equatorial Currents could

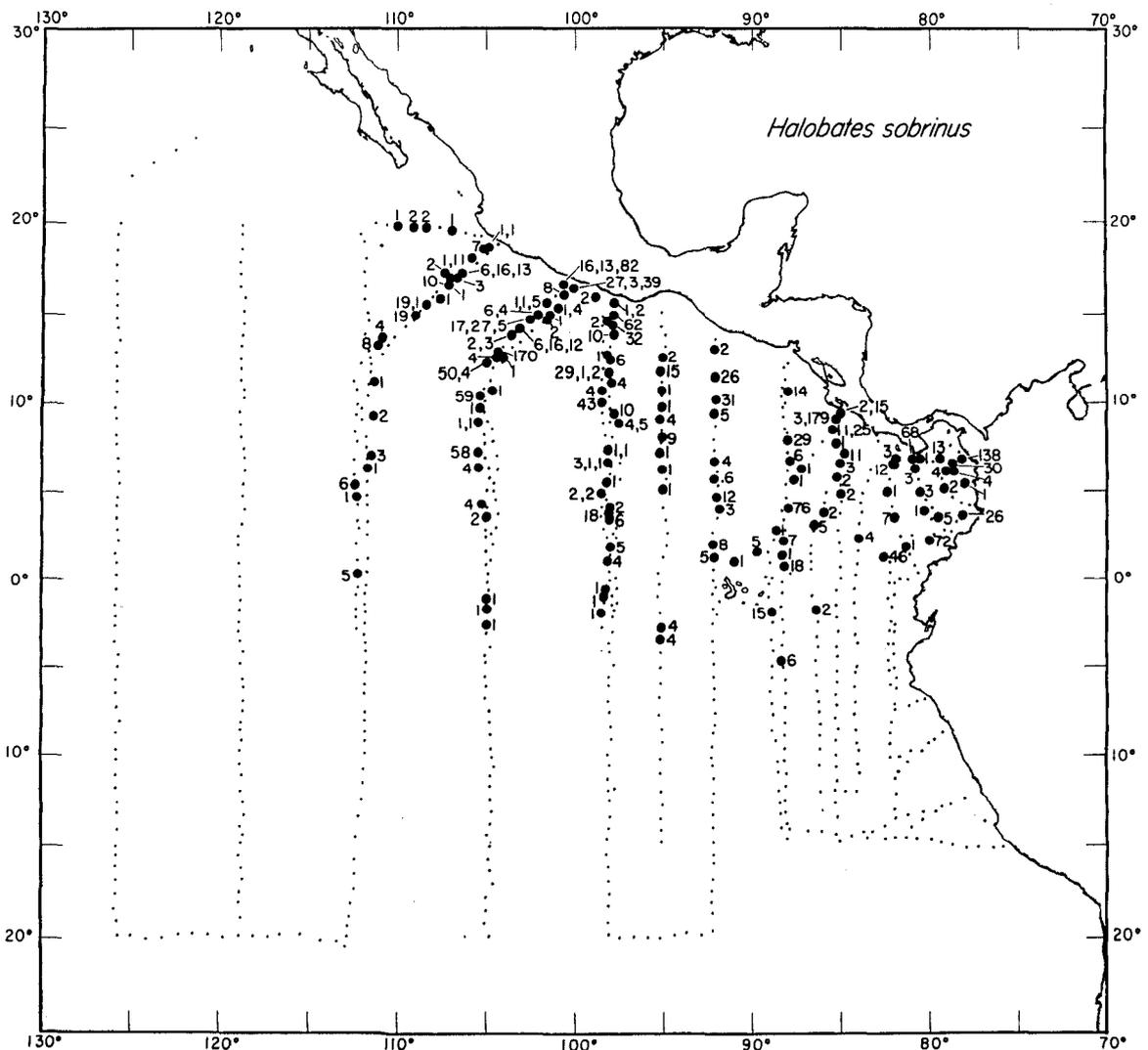


FIGURE 4.—*Halobates sobrinus* distribution, as in Figure 3.

carry the species westward (Sverdrup et al. 1942), its range shows no such effect (Figures 2, 4). More samples from the central equatorial Pacific are needed to confirm the apparent abrupt termination of the species' range at about long. 112° W. In the EASTROPAC area, *H. sobrinus* does not occur west of about long. 112° W or south of lat. 5° S (Figure 4). While the ranges of *H. sobrinus* and *H. micans* overlap somewhat, their regions of high population density (defined as samples with ≥ 10 individuals) overlap very little (Figure 5).

Halobates sericeus is clearly confined to the central watermasses of the North and South

Pacific. The three records of this species on the Equator (at long. 82° W, 119° W, and 129° W; Figure 2) appear likely to be misidentifications (data from Herring 1961). However, present data also include one individual which lies well outside the apparent range of the species (Figure 6; at long. 100° W, lat. 16° N) and we have reconfirmed the identification of this specimen. Since these insects are usually < 4 mm long, individuals may be carried long distances by the wind. This could explain such isolated captures. *Halobates sericeus* does not occur in the upwelling areas of the eastern tropical Pacific, nor in the zonal equatorial currents (Fig-

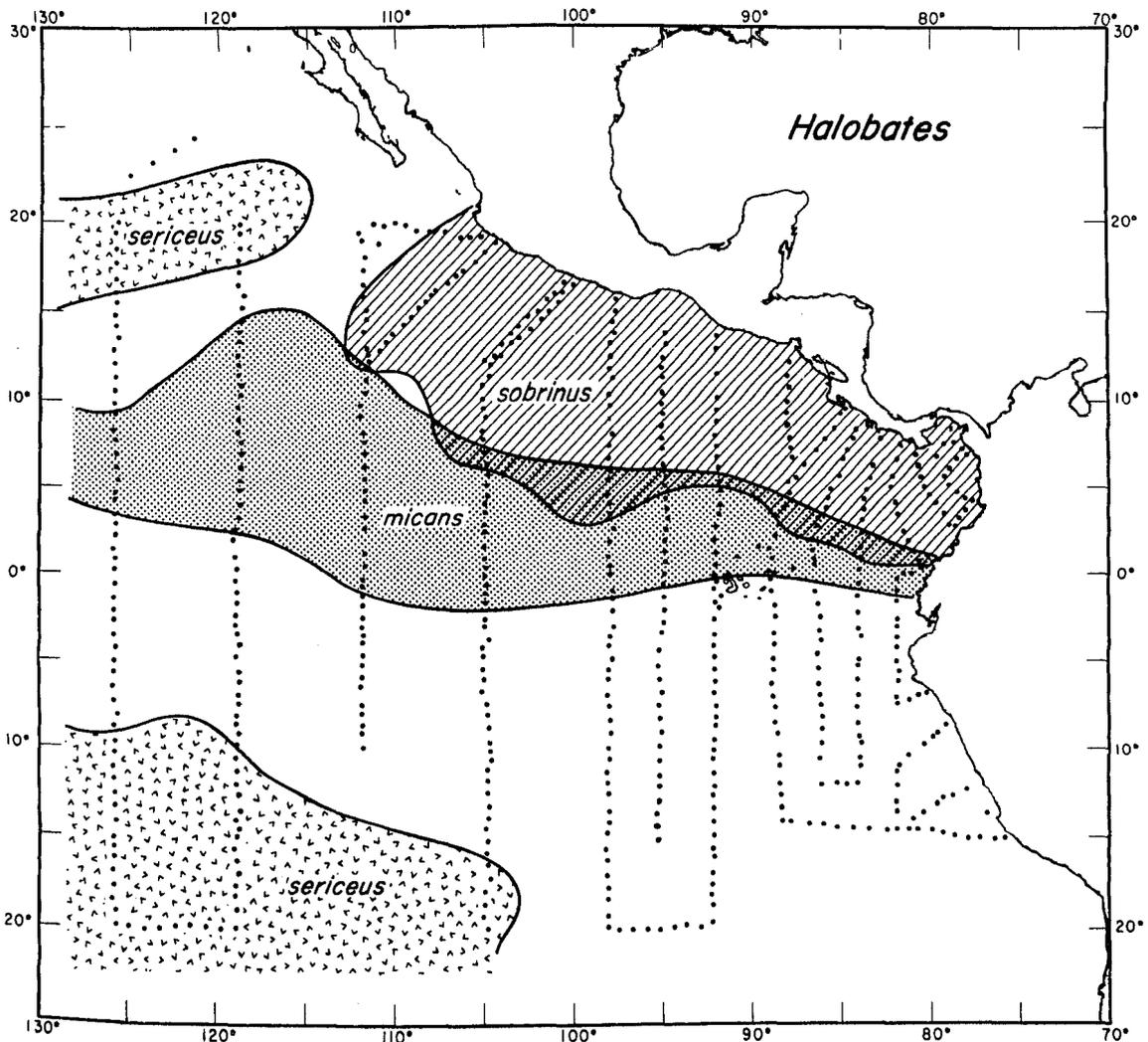


FIGURE 5.—Areas of high population densities of three *Halobates* species in the EASTROPAC area. "High" is defined as occurrence of $N \geq 10$ individuals in at least one sample (area per sample $\approx 1,800$ m²).

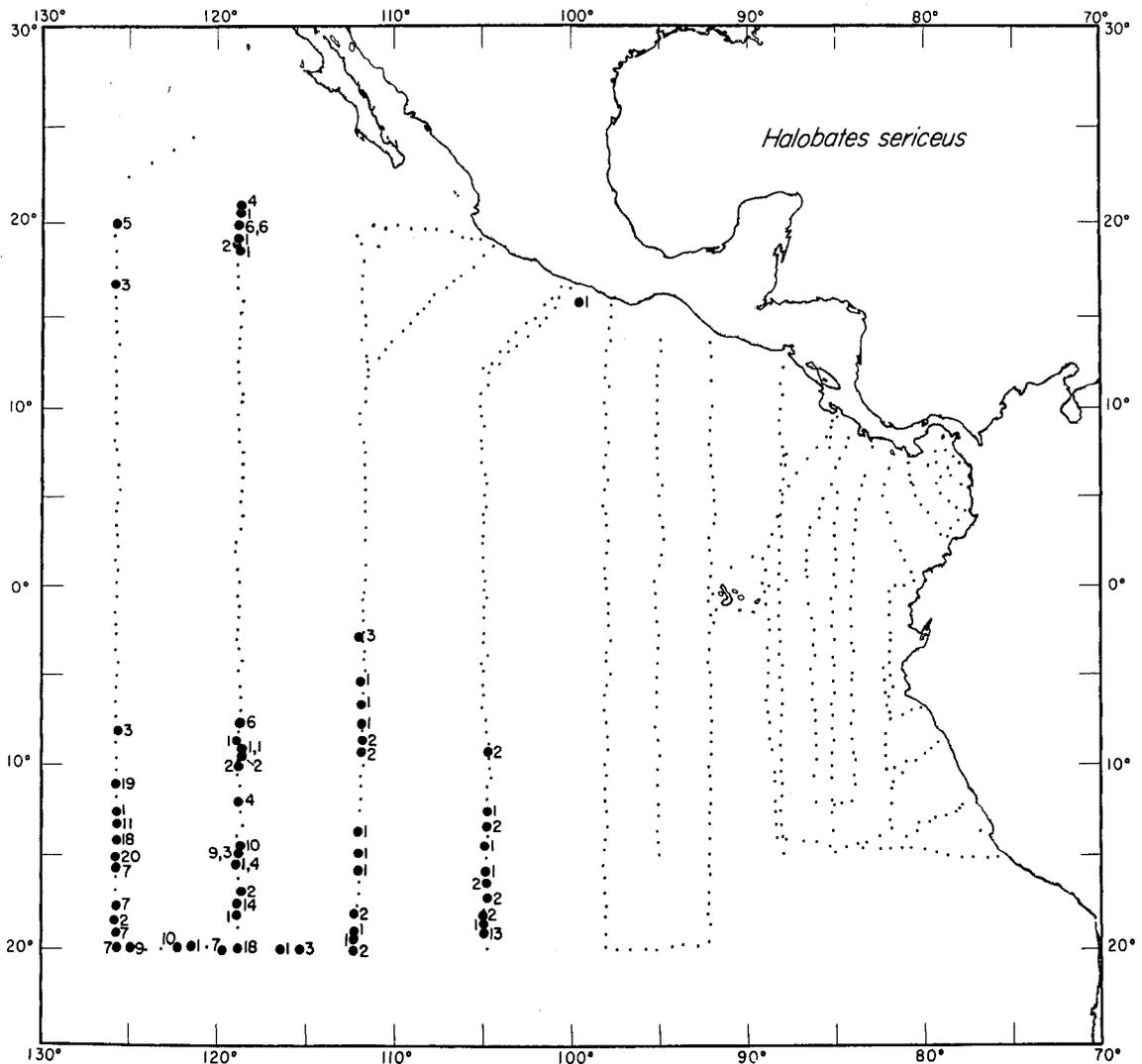


FIGURE 6.—*Halobates sericeus* distribution, as in Figure 3.

ure 6). It occurs completely outside the range of *H. sobrinus* (Figures 4, 5) and shows only very small overlap with *H. micans* (Figures 3, 5).

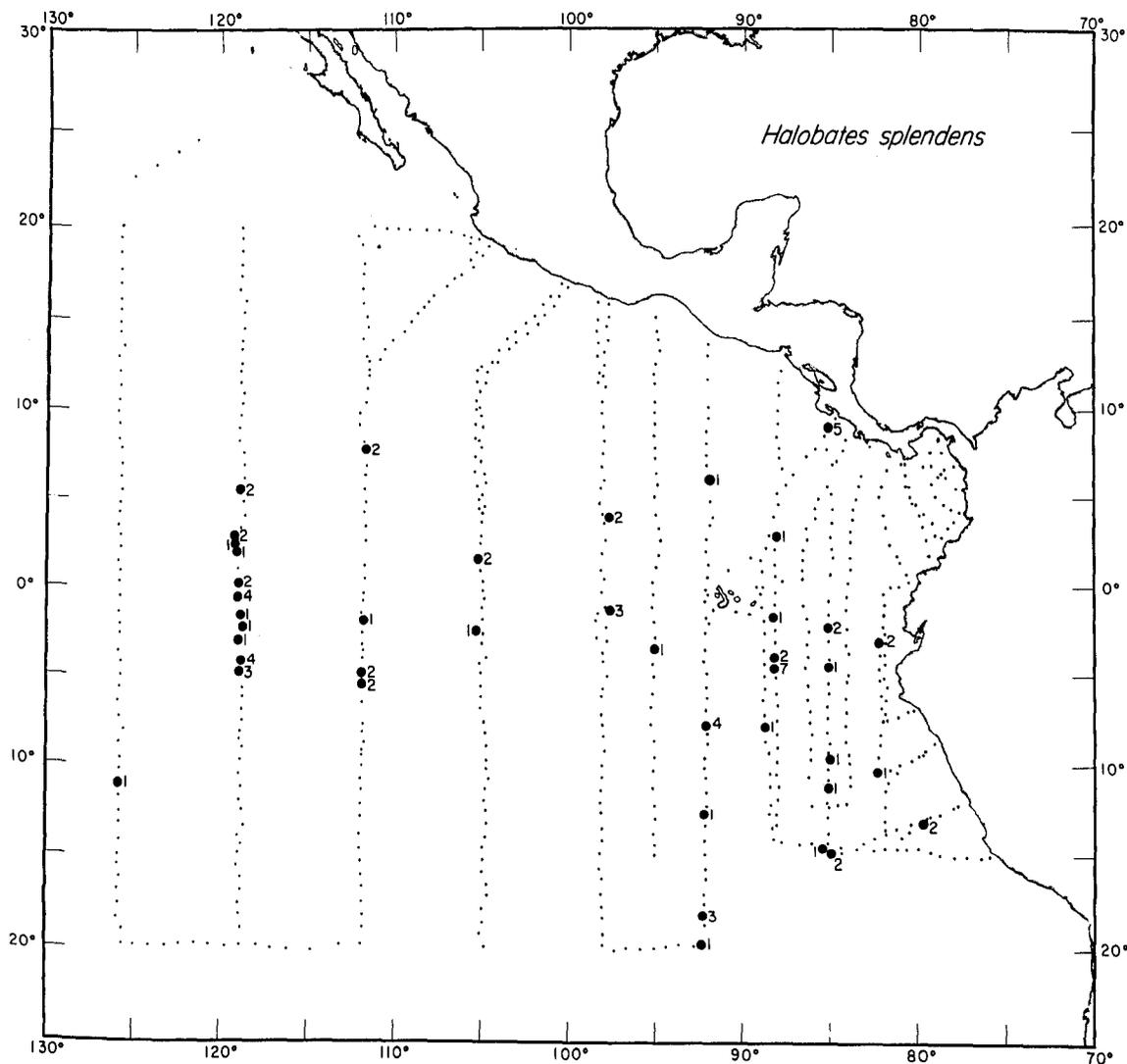
Halobates splendens, rarest of the four EASTROPAC species, has not been found north of about lat. 8°N (Figure 7). The captures reported in the Chile Current (Figure 2) indicate that this species may be primarily associated with the central South Pacific watermass or the South American coastal current System. Sampling in this region is insufficient at present to permit better definition of its range.

The distributions of *Halobates* spp. appear to be

controlled by two major influences: 1) the patterns agree with broad, general surface-circulation patterns, and 2) species' regions of high abundance generally tend not to overlap. We do not know whether the nonoverlap is due to competitive effects or to physiological adaptations by each species to a particular environmental regime.

Abundance

Two important difficulties in deriving quantitative estimates of *Halobates* spp. abundance are: 1) most neuston nets (including ours) tend to skip out

FIGURE 7.—*Halobates splendens* distribution, as in Figure 3.

of the water in anything except calm weather, making estimation of area sampled or volume filtered difficult; and 2) these insects are known to avoid nets but the extent of avoidance is unknown (Cheng 1973c; Cheng and Enright 1973). However, the samples used in this study resulted from replicate tows and may therefore be reasonably compared with one another and used to set lower limits on abundance.

Our data showed that in *H. micans*, *H. sobrinus*, and *H. splendens* numbers of adults are about twice that of nymphs (Table 2). This may be a result of several factors: 1) nymphs might avoid

the net more actively than adults (unlikely); 2) nymphs are smaller than adults and may wash through the meshes of the net more easily (possible); 3) nymphs might have been missed in sorting (unlikely; samples have been rechecked); and 4) aspects of their natural history might produce such a distribution (e.g., heavy predation on nymphs plus long life-span of adults). Data do not exist to test hypotheses 1) and 4). We can offer no explanation for the differences between *H. sericeus* and the other species.

Since *H. micans* and *H. sobrinus* accounted for almost 90% of total individuals caught (65.6 and

TABLE 2.—Numbers of *Halobates* spp. caught in the EASTROPAC area. Roman numerals = nymphal instar number.

Species	Individuals	Adults	Nymphs	Numbers per life stage					Adults	
				I	II	III	IV	V	♂	♀
<i>H. micans</i>	754	490	264	22	15	45	83	99	204	286
<i>H. sobrinus</i>	2,156	1,388	768	63	75	179	178	273	693	695
<i>H. sericeus</i>	285	126	159	19	20	34	31	55	55	71
<i>H. splendens</i>	77	50	27	0	5	6	8	8	20	30

23.3%, respectively), we will confine further discussions of abundance to these two species.

In an attempt to determine if *H. micans* and *H. sobrinus* are randomly distributed on the ocean surface, curves of "number per tow" vs. "number of tows with that number of insects" were compared with Poisson probability density functions. Such tests are appropriate for these data (Sokal and Rohlf 1969) but difficult to perform because of uncertainty as to how many "zero" catches should be included in the divisor when calculating a mean catch-per-tow. Maximum likelihood estimates of the means for truncated Poisson distributions (i.e., lacking a zero class) were therefore calculated for both species (Cohen 1960), and the frequency distributions of Figure 8 were compared with the calculated (expected) Poisson distribution. Chi-square tests of expected vs. observed were very highly significant for both species ($P < .001$), leading to the rejection of the null hypothesis that observed distribution cannot be told from a Poisson. We therefore conclude that both *H. micans* and *H. sobrinus* are nonrandomly distributed

across the ocean surface in the regions where they occur.

The coefficient of dispersion (s^2/\bar{x} , Sokal and Rohlf 1969) for *H. sobrinus* is ≈ 46.0 and for *H. micans* is ≈ 5.8 . We thus conclude that both species are very strongly clumped ("patchy"), *H. sobrinus* more so than *H. micans*. The numbers per sample also vary widely, e.g., from 0 to 179 for *H. sobrinus*. It is not known what environmental factors cause one location to provide higher catches than another. Assuming optimum sampling conditions (perfect net performance, etc.), the highest population densities calculatable for each of the four species are presented in Table 3. These are lower limits because of probable net avoidance

TABLE 3.—Highest estimates of population density for *Halobates* spp. in the EASTROPAC area.

Species	Maximum no./sample	Maximum observed population (no./km ²)
<i>H. micans</i>	39	2×10^3
<i>H. sobrinus</i>	179	1×10^4
<i>H. sericeus</i>	20	1×10^3
<i>H. splendens</i>	7	4×10^2

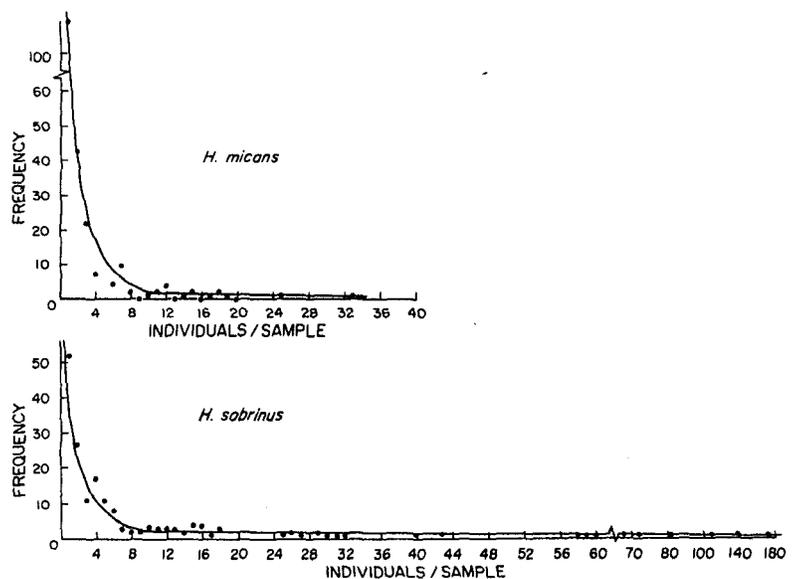


FIGURE 8.—Frequency distribution of *Halobates micans* and *H. sobrinus* in positive samples. The number of insects caught per tow is plotted against the number of tows containing that many insects. "Zero catches" are excluded (see text).

behavior (Cheng 1973c; Cheng and Enright 1973). Actual maximum densities are probably considerably higher.

Cooccurrence

The incidence of cooccurrence of two or more *Halobates* spp. in our samples was low. Out of 498 positive samples, only 33 contained two species (Table 4); 1 sample had three species. This confirms the impression given by distributional maps (Figures 2-7) that the various species seldom occur together. Separation of distribution holds, even for species with overlapping ranges (*H. micans* and *H. sobrinus*). In those samples in which these two species cooccur, there is no correlation of abundance (Figure 9). This indicates that local variations in abundance of these two species are not merely responses to vectorial (i.e., physical) forces. If vectorial forcing were the case, then the two species should be abundant in the same samples and be positively correlated when they cooccur.

The mean number of individuals per positive tow (pooled for all cruises and by cruise) is much higher in *H. sobrinus* than in *H. micans*, although the percentage of positive tows is similar for both species (Table 5). However, the highest frequency of capture (i.e., percentage of positive tows) for *H. sobrinus* occurred in the same series as the lowest frequency for *H. micans* (Figure 10). This may represent some temporal partitioning of resources, but is undoubtedly partly a function of the species' nonoverlapping centers of high abundance

TABLE 4.—Cooccurrences of *Halobates* spp. in 498 positive EASTROPAC samples (at least one specimen of each species per sample).

Species	<i>H. micans</i>	<i>H. sobrinus</i>	<i>H. sericeus</i>	<i>H. splendens</i>
<i>H. micans</i>	—	28	1	1
<i>H. sobrinus</i>	—	—	0	4
<i>H. sericeus</i>	—	—	—	1
<i>H. splendens</i>	—	—	—	—

TABLE 5.—Occurrence of *Halobates micans* and *H. sobrinus* by EASTROPAC cruise series.

Cruise series	<i>H. micans</i>			<i>H. sobrinus</i>		
	No. positive tows	Total no. insects	Mean no. insects/tow	No. positive tows	Total no. insects	Mean no. insects/tow
10	76	387	5.1	50	568	11.4
20	23	43	1.9	28	436	15.6
30	8	10	1.3	17	65	3.8
40	17	61	3.6	30	446	14.9
50	20	45	2.3	18	192	10.7
60	22	50	2.3	5	20	4.0
70	52	196	3.8	29	382	13.2
Totals	218	792	3.6	177	2,109	11.9
Positive tows, %	13.2			10.7		

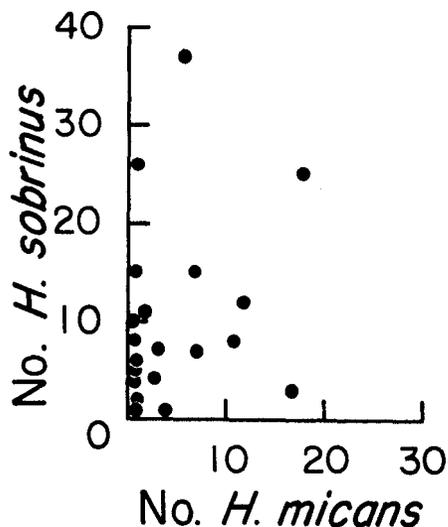


FIGURE 9.—Abundance of *Halobates micans* and *H. sobrinus* in samples in which the species cooccurred. Abundance of the two species is not correlated (Olmstead and Turkeys' corner test for associativity, $P > 0.05$).

(Figure 5), differences in cruise tracks, and differences in times of the year (Figure 1).

Temperature Effects

Temperature of surface waters appears to be important in the distribution of *Halobates* spp. Figure 11 shows the number of individuals per positive sample plotted against surface water temperature for both March and August 1967. Abundance was very low in samples taken at $<24^{\circ}\text{C}$ and $>28^{\circ}\text{C}$. The optimal temperature band appears to be quite narrow. The shape of these curves is not an artifact of the number of samples obtained at each temperature: the data have been standardized to a per tow basis and there were many tows taken at each temperature.

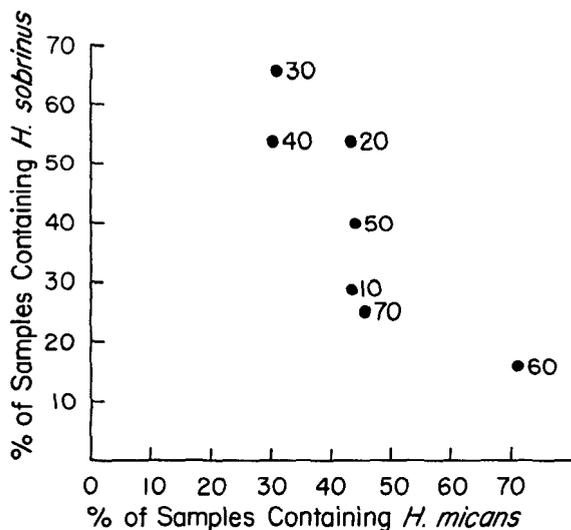


FIGURE 10.—Percentage of samples containing *Halobates micans* and *H. sobrinus* compared by cruise series (Table 1). Series numbers are shown beside each point. Note inverse relationship.

CONCLUSIONS

Four pelagic species of *Halobates*—*H. micans*, *H. sericeus*, *H. sobrinus*, and *H. splendens*—are found in the eastern tropical Pacific area. Within the EASTROPAC area, the ranges of the four species

agree well with dominant oceanic zones or domains; e.g., tropical-equatorial, central water-mass, and coastal upwelling. The worldwide distributions of the four species in the Pacific Ocean have also been found to agree with recognized oceanic domains (Herring 1961; Savilov 1967) although at present data are still insufficient to clearly define some boundaries, especially in the southern tropical Pacific. Although species may cooccur in the EASTROPAC area, geographical regions of high abundance for *H. micans*, *H. sobrinus*, and *H. sericeus* show little overlap. Our estimates for maximum abundance (lower bounds) for the two more abundant species, *H. micans* and *H. sobrinus*, are 400-10,000/km². This is likely to be conservative because they can avoid nets and because the neuston net used in our study did not sample in an ideal manner. We found *Halobates* to be most abundant in 24°-28° C waters. The two abundant species showed very patchy distributions. Present temporal and spatial coverages are insufficient to allow us to define possible seasonal variations in population density or structure.

It seems clear that the distributions of *Halobates* spp., inhabiting a strictly two-dimensional world, are governed by the same oceanic processes which shape the distributions of other marine species that inhabit a three-dimensional world.

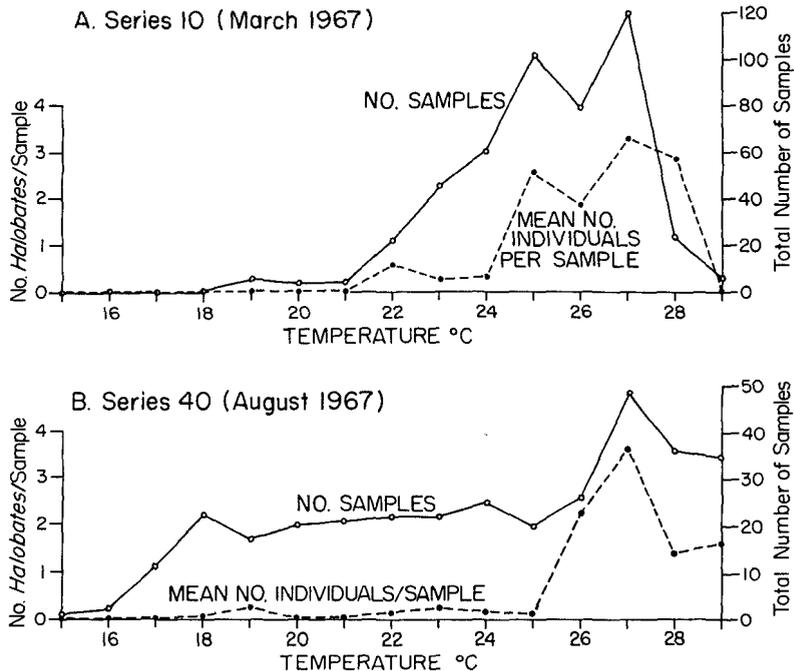


FIGURE 11.—Number of *Halobates* specimens (data for all four species combined) per positive sample vs. sea-surface temperatures. A. Series 10, March 1967. B. Series 40, August 1967. (Exact dates and area covered given in Table 1 and Figure 1.)

ACKNOWLEDGMENTS

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